

## PATTERNS OF AVIAN GEOGRAPHY AND SPECIATION IN THE INTERMOUNTAIN REGION

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**ABSTRACT.**—The Intermountain Region comprises a huge arena where major avifaunas more highly developed beyond the Great Basin come into contact. For this reason the distribution and composition of avifaunas in riparian and pinyon-juniper woodlands and in coniferous forests in this region are understood most clearly if considered as part of a broader system of patterns evident in western North America. Riparian woodland samples point to a complex meeting ground in the Intermountain Region of two major avifaunas of equivalent size, but from opposite distributional backgrounds. These northern and southern avifaunas do not mix among the samples represented except in western Nevada where two species of ultimate southern origin have penetrated a basically northern avifauna. Approaching the Great Basin, from the two centers of abundance of riparian species in the Snake and Colorado River drainages, species richness drops. Habitat depletion and, to a lesser extent, insularity play roles in this impoverishment. In the most depauperate riparian avifaunas, six species commonly coexist, each in a different family. Comparison of the pinyon zone avifaunas of two groups of mountain ranges, 90 km apart along the California-Nevada border, demonstrates a striking trade off among species of northern and southern biogeographic histories. The northern or Boreal forms, many of which are numerous in the Sierra Nevada, have had easy access to the favorable, cool, and relatively moist pinyon forests in the adjacent spur ranges. In contrast, the species of southern or Austral derivation prefer the warm and very arid pinyon woodland a short distance to the south. Few species are confined to either northern or southern sites, overlap in species composition is great, and equivalent species richness is achieved. However, despite these similarities, strong geographic differences in abundance of most species in each pinyon avifauna and the occurrence of at least 12 specific and subspecific range boundaries suggest the interposition between northern and southern pinyon areas of a substantial, but as yet poorly characterized, climatic barrier. Boreal species richness declines abruptly from high values in the southern Cascades and Sierra Nevada to low levels in a zone of impoverishment across western and central Nevada. From near 116° W Longitude in eastern Nevada, coincident with the appearance of fir and/or bristlecone pine forests, species numbers climb gradually until the main Rocky Mountains are reached. There, species richness compares favorably with that in the Sierra Nevada. The proportion of species favoring riparian woodlands over coniferous forests is higher on the island mountaintops of the Great Basin than in the Boreal "continents" of the Sierra Nevada-Cascades and Rocky Mountains. The western edge of the Great Basin richly demonstrates examples of stages in avian speciation. A full range of interactions is represented, from intergradation of poorly characterized races, through abrupt zones of hybridization between strongly marked subspecies of different racial complexes or of semispecies, to sympatry and infrequent interbreeding of closely-related, full species in recent secondary contact. These various zones of population interaction coincide strikingly with sharp floristic and climatic gradients. A major avifaunal break occurs between coastal or Sierra Nevada forms that inhabit oak-chaparral and/or coniferous forest and closely-related interior forms that prefer pinyon-juniper or aspen-willow associations. In keeping with the special requirements of each species, contact zones and areas of disjunction show general, rather than precise, coincidence in the western Great Basin. There is no Great Basin Boreal Avifauna; the most distinctive interior forms occur across the entire span from eastern California to Colorado. The low desert trough along the east side of the Sierra Nevada that divides major mountain systems in the western portion of the Intermountain Region is not the principal barrier dividing coastal Sierra Nevada from interior avifaunas. Instead, the major avifaunal transition occurs in a belt of variable width just east of the crest of the Cascade Mountains and Sierra Nevada, where the precipitation shadow and continental climate begin to exert crucial influence.

Although much neglected in the past because of difficulty of access and false impressions of biotic sterility, the Inter-

mountain Region of western North America is emerging as a fascinating natural laboratory requiring the close attention of the

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biogeographer-ecologist. Islands of conifers or aspen, cool mountain meadows, and attendant biotas on scores of mountaintops lie isolated by seas of desert from source stocks in the Sierra Nevada and Rocky Mountains. The unique physical setting of a multiplicity of more or less parallel ranges, each differing in size, geology, and configuration from adjacent ones, cannot be duplicated elsewhere among continental mountain systems. And, because of low human density, many of the montane habitats are relatively undisturbed, thus permitting a good look at original, man-unmodified distributions of species. In the valleys as well, oases offer insular environments for a variety of organisms whose interrupted ranges intrigue the biogeographer.

With increased field efforts by a number of workers in recent decades, the bird species breeding on many of the major basin ranges have been tallied, and information has reached a level allowing tests of certain fundamental theories of insular biogeography (Johnson 1975). However, these tests are just the beginning. With additional "alpha" exploration in the future, the enlarged data base will permit more diverse and detailed kinds of analyses. But, already enough distributional information has accumulated to suggest several patterns that challenge the avian geographer. In this paper I identify and discuss these patterns in a search for common biogeographic themes. Furthermore, I specify among the birds of the Intermountain Region distributional situations relevant to hypotheses on the control of range boundaries. Finally I describe the prominent zone of active speciation in the western part of the region and attempt to interpret this zone in relation to coincident physiographic, climatic, and floral discontinuities.

Nomenclature and sequence of species follow the checklist of North American birds except where superceded by the 32nd supplement (American Ornithologists' Union 1957, 1973).

#### AVIFAUNAL TRANSECTS IN THE INTERMOUNTAIN REGION

Riparian woodlands in valleys and canyons, pinyon woodlands on mountainsides, and coniferous forests and aspen on mountaintops comprise the major habitats for birds in the region between the axis of the Sierra Nevada-Cascade Range and the Rocky Mountains. Analyses of the richness and composition of selected avifaunas breeding in sample areas of these woodlands and forests expose several patterns that elucidate the fundamental organization of avian distribution in the region. Moreover, these samples along transects demonstrate the complex modes by which historical aspects of avifaunal distribution influence present-day patterns of species richness and community structure. Figure 1 shows the location of the sample areas and their basic avifaunal relationships.

#### Latitudinal Variation in Riparian Woodland Avifaunas

Bird species requiring riparian vegetation for breeding occur discontinuously in cottonwoods, willows, ashes, and associated thickets along watercourses and at valley oases throughout the Great Basin region. When species of land birds breeding in such habitats are compared (Table 1), among 11 sample areas from the Snake River drainage in the north to the Colorado River drainage in the south, prominent differences and some unexpected similarities emerge in total species numbers, composition of the avifaunas according to evolutionary derivation, and structure of the avifaunas by ecologic roles. That these three topics are interrelated will become evident in the discussion to follow.

*Total species numbers.*— Of immediate interest is the striking similarity of the geographically extreme stations, Central Idaho and Colorado River, in species richness, 28 versus 25, from the pool of 43 species. But, upon entering the Great Basin from the Snake River drainage, species totals drop, to

21 in the Elko sample, 17 in Humboldt, 15 in Toiyabe, and to 12 in Kawich. Similarly, moving north from the Colorado River, total species numbers fall to 13 in Pahrnagat, 12 in Meadow Valley Wash, and 11 at Ash Meadows-Pahrump. Figure 2 demonstrates the strong and abrupt avifaunal attenuation

that occurs with increasing distance from the lush riparian woodlands to the north and south. The smallest tallies, for the Kawich area and Ash Meadows-Pahrump, probably reflect habitat impoverishment in view of the limited extent and interrupted growth of the riparian clumps there. For

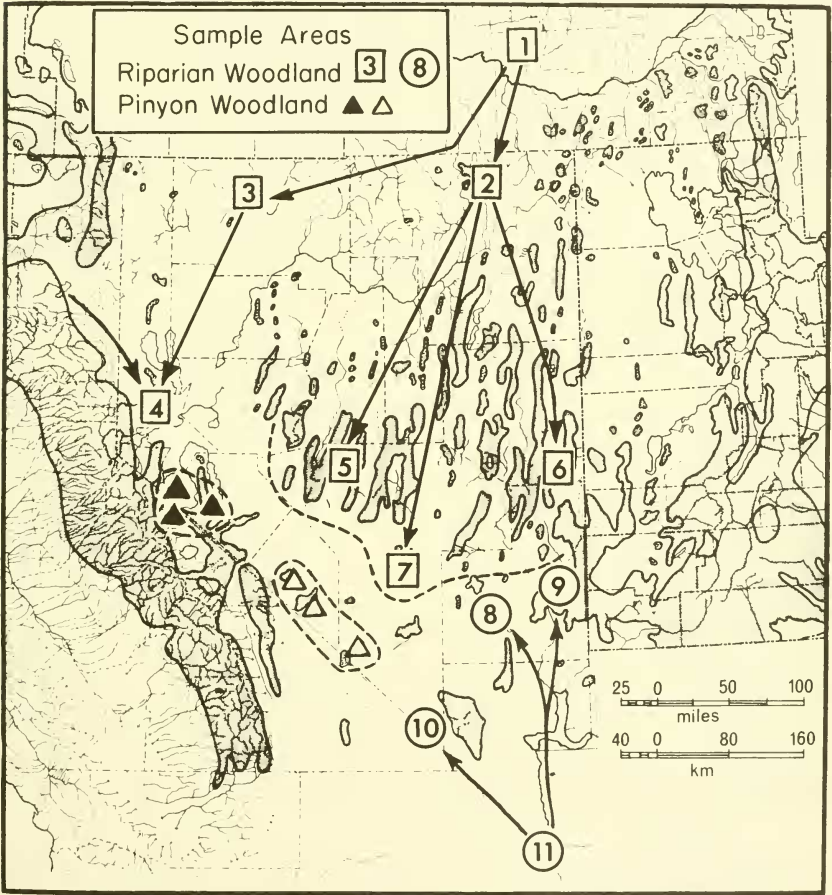


Fig. 1. Sample areas of riparian woodland (squares and circles) and pinyon woodland (triangles) avifaunas in the Intermountain Region. Shading grossly defines regions of forest and woodland. Numbers in squares or circles correspond to those of sample areas in Table 1. Arrows indicate closest avifaunal relationships. Northern and southern pinyon areas are denoted by solid and open triangles, respectively. Approximate boundary of northern and southern riparian woodland avifaunas is shown by the dashed line between samples 7 and 8.

TABLE 1. Species breeding in riparian woodlands at selected localities in the Intermountain Region<sup>1</sup>.

	1	2	3	4	5	6	7	8	9	10	11
	Central Idaho	Elko	Humboldt	Truckee-Carson	Toiyabe	Ely	Kawich	Pahranagat	Meadow Valley Wash	Ash Meadows-Pahrump	Colorado River
<b>Northern Element</b>											
<i>Coccyzus erythrophthalmus</i>	X	—	—	—	—	—	—	—	—	—	—
<i>Dendrocopos villosus</i> <sup>2</sup>	X	X	X	X	X	X	X	—	—	—	—
<i>Dendrocopos pubescens</i> <sup>2</sup>	X	X	X	X <sup>3</sup>	—	X	—	—	—	—	—
<i>Tyrannus tyrannus</i>	X	—	X	— <sup>4</sup>	—	—	—	—	—	—	—
<i>Iridoprocne bicolor</i>	X	X	—	X	—	X	—	—	—	—	—
<i>Parus atricapillus</i> <sup>2</sup>	X	X	—	—	—	—	—	—	—	—	—
<i>Troglodytes aedon</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Dumetella carolinensis</i>	X	—	—	—	—	—	—	—	—	—	—
<i>Turdus migratorius</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Catharus fuscescens</i>	X	X	—	—	—	X	—	—	—	—	—
<i>Catharus ustulatus</i>	X	X	X	X	X	X	—	—	—	—	—
<i>Vireo gilvus</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Vireo olivaceus</i>	X	—	—	—	—	—	—	—	—	—	—
<i>Vermivora celata</i>	X	X	X	—	X	X	—	—	—	—	—
<i>Oporornis tolmiei</i>	X	X	X	X	X	X	X	—	—	—	—
<i>Stetophaga ruticilla</i>	X	—	—	—	—	—	—	—	—	—	—
<i>Passerella iliaca</i>	X	X	X	X	X	X	—	—	—	—	—
<b>Southern Element</b>											
<i>Zenaidura macroura</i>	—	—	—	—	—	—	—	— <sup>4</sup>	—	— <sup>4</sup>	X
<i>Dendrocopos scalaris</i> <sup>2</sup>	—	—	—	—	—	—	—	X	X	—	X
<i>Centurus uropygialis</i> <sup>2</sup>	—	—	—	—	—	—	—	—	—	—	X
<i>Sayornis nigricans</i>	—	—	—	—	—	—	—	X	X	—	X
<i>Pyrocephalus rubinus</i> <sup>2</sup>	—	—	—	—	—	—	—	X	—	X	X
<i>Thryomanes bewickii</i> <sup>2</sup>	—	—	—	X <sup>3</sup>	—	—	—	X	X	X	X
<i>Toxostoma dorsale</i> <sup>2</sup>	—	—	—	—	—	—	—	—	—	X	X
<i>Sialia mexicana</i>	—	—	—	X <sup>3</sup>	—	—	—	—	—	—	—
<i>Phainopepla nitens</i> <sup>2,5</sup>	—	—	—	—	—	—	—	— <sup>5</sup>	—	— <sup>4</sup>	X
<i>Vireo bellii</i>	—	—	—	—	—	—	—	—	—	X <sup>4</sup>	X
<i>Vermivora luciae</i>	—	—	—	—	—	—	—	— <sup>5</sup>	X	—	X
<i>Icterus cucullatus</i>	—	—	—	—	—	—	—	—	X	X	X
<i>Piranga rubra</i>	—	—	—	—	—	—	—	— <sup>5</sup>	—	X	—
<i>Guiraca caerulea</i>	— <sup>5</sup>	—	—	—	—	—	—	X	X	X	X
<i>Pipilo aberti</i>	—	—	—	—	—	—	—	—	X	—	X
<b>Widespread Element</b>											
<i>Falco sparverius</i> <sup>2</sup>	X	X	X	X	X	X	X	X	X	X	X
<i>Coccyzus americanus</i>	X	—	—	X	—	—	—	X	—	X	X
<i>Otus asio</i> <sup>2</sup>	X	—	—	X	—	—	—	X	X	—	X
<i>Archilochus alexandri</i>	X	X	—	X	—	X	—	X	—	—	X
<i>Colaptes auratus</i> <sup>2</sup>	X	X	X	X	X	X	X	—	X	—	X
<i>Tyrannus verticalis</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Empidonax traillii</i>	X	X	— <sup>5</sup>	X	— <sup>5</sup>	—	—	—	—	X	X
<i>Dendroica petechia</i>	X	X	X	X	X	X	X	—	—	—	X
<i>Icteria virens</i>	X	X	X	X	X	X	X	X	—	—	X
<i>Icterus galbula</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Melospiza melodia</i> <sup>2</sup>	X	X	X	X <sup>4</sup>	X	X	X	X	—	— <sup>5</sup>	X
<b>TOTALS</b>	<b>28</b>	<b>21</b>	<b>17</b>	<b>22</b>	<b>15</b>	<b>19</b>	<b>12</b>	<b>13</b>	<b>12</b>	<b>11</b>	<b>25</b>

<sup>1</sup>Sources of data on occurrence as follows: (1) Central Idaho, a composite list from several localities in the center of the state, taken from Burleigh (1972); (2) Elko, a composite list from field notes and specimens in the Museum of Vertebrate Zoology (= MVZ) from the northern portion of Elko County, and from Linsdale (1936); (3) Humboldt, from Taylor (1912); (4) Truckee-Carson, a composite list from original data of author (= NKJ) and from Linsdale (1936); (5) Toiyabe, from Linsdale (1936); (6) Ely, data from Spring and Steptoe valleys, NKJ; (7) Kawich, NKJ; (8) Pahranagat, NKJ and MVZ; (9) Meadow Valley Wash, NKJ and Linsdale (1936); (10) Ash Meadows-Pahrump; (11) Colorado River, NKJ and Grinnell and Miller (1944). Species that typically prefer or require riparian woodland are included.

<sup>2</sup>Permanently-resident species.

<sup>3</sup>Form shows closest affinity to populations in California, to the northwest.

<sup>4</sup>Former or casual occurrence.

<sup>5</sup>Recorded during the breeding period, but not proved to be nesting.



Ash Meadows-Pahrump and Pahrnatag samples, we also may be seeing the effects of insularity. Several Colorado River drainage species, such as the Abert's Towhee (a highly sedentary, permanently resident form), probably have had great difficulty colonizing the isolated riparian areas to the north. However, one could also argue that this and other potential colonists are missing from these remote areas because the proper kinds of riparian habitats, as found along the Colorado River and its tributaries, are lacking.

The moderate size (22 species) of the Truckee-Carson sample reflects its position at the well-watered eastern base of the Carson Range.

*Origin of riparian woodland avifaunas.*—The entire riparian woodland avifauna can be divided on the basis of evolutionary

background or derivation into (1) a northern element consisting of species with northern centers of distribution and affinities, (2) a southern element comprised of species with southern distributional relationships, and (3) a widespread element including species occurring throughout the western United States or beyond. The species are grouped in Table 1 according to these three elements. Note that none of the species of the northern element occurs in any samples south of Kawich and, with one exception (see below), none of the species of the southern element is found in any samples north of Meadow Valley Wash or Pahrnatag. Therefore, the two major avifaunas approach, but do not contact and intermix, in the southern Intermountain Region.

Although basically of northern derivation, the riparian avifauna of the Truckee-Carson sample is of special interest because it contains a distinctive group of four species with affinities to populations of northeastern California. One of these species, the Downy Woodpecker, is of northern affinity; two species, the Western Bluebird and Bewick's Wren, are of southern derivation. The Song Sparrow is widely distributed. The western Nevadan populations of these four species probably originated from stocks in the Central Valley of California, stocks that spread into the western Great Basin via the Modoc Plateau.

The widespread component comprises between 39 and 62 percent of each sample (Fig. 2). No clear evidence of differential decline of northern (or southern) versus widespread elements is shown as the zone of impoverishment is approached. Thus, the diminution is general and involves approximately equivalent shrinkage of the two major components of each avifauna.

*Community structure and ecologic roles.*—A surprising finding is that the widespread species fraction seems to have stabilized, at either seven or five species, for the five sample areas with the smallest numbers of species. Thus, the Humboldt, Toiyabe, and Kawich samples have seven widespread spe-

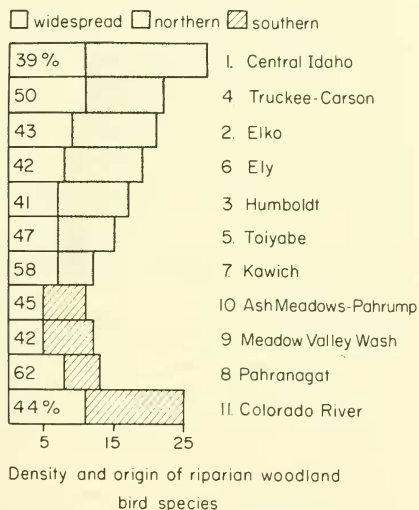


Fig. 2. Percent composition, according to geographic derivation, of avifaunas in 11 riparian woodland sample areas. These are arranged in order of decreasing avifaunal size (species density) toward the boundary of northern and southern avifaunas, between Kawich and Ash Meadows-Pahrump. For example, the Colorado River sample has 25 species, 11 (= 44 percent of which are widespread and 14 (= 56 percent) of southern derivation.

cies in addition to northern ones. And, the lists of species are identical! The Ash Meadows-Pahrump and Meadow Valley Wash samples include southern species and five that are widespread. However, in these two samples the coincidence in identity of widespread forms is incomplete; each shares three of their five species.

Six of the 11 widespread species, *Falco sparverius*, *Colaptes auratus*, *Tyrannus verticalis*, *Icteria virens*, *Icterus galbula*, and *Melospiza melodia*, occur in nine or more sample areas. Because these species commonly coexist, they form a group of great interest. I view them as a "standard riparian woodland species" group analogous to the "standard Boreal species" group I identified in montane habitats of the western United States (Johnson 1975). Note that each of the six species is in a different family. Therefore, coexistence in the riparian woodland avifaunas examined here predominates among species of fundamentally different body designs.

Included in the tallies of Table 1 are five pairs of closely related species, three pairs of which are congeneric. Furthermore, within each pair, each species is from a different distributional element. The pairs are *Coccyzus erythrophthalmus*, and *C. americanus*, *Dendrocopos pubescens* and *D. scalaris*, *Tyrannus tyrannus* and *T. verticalis*, *Troglodytes aedon* and *Thryomanes bewickii*, and *Dendroica petechia* and *Vermivora luciae*. Not all of the species of each pair contact locally, but the interactions of those that do meet would merit close study. Indeed, a fertile field awaits the ecomorphologist willing to analyze community structure, foraging roles, and morphologic adaptations among the coexisting species of birds in any of the riparian woodlands discussed.

#### Latitudinal Variation in Pinyon Woodland Avifaunas

Among arboreal habitats, groves of single-leaf pinyon (*Pinus monophylla*) comprise the most extensive formation in the Inter-

mountain Region, and these woodlands therefore represent an important habitat for breeding birds. Typically this pine is scattered over mountain slopes in open stands or clumps of small trees with much intervening brush. Occasionally, on favorable sites, growth can be luxuriant, and true forest is achieved. Here trees grow to heights of 10 m or more, and the closed canopy shades a needle-strewn forest floor. This site-to-site variability in growth form of pinyon intrigues the ornithologist because, as has long been known, birds clearly respond to physical features of vegetation. A second noteworthy aspect of pinyon is the wide elevational range often occupied on a single mountainside. In the White Mountains, California, for example, pinyon occurs from approximately 2000 to 2900 m, with the best development between 2450 and 2600 m (St. Andre et al. 1965).

In the Grapevine Mountains of southern Nye County, Nevada, these variable characteristics of pinyon are seen clearly (Miller 1946). Small, scrubby trees grow in scattered stands, exceptionally fine tracts of old trees with trunks two feet in diameter form forests locally on the high northeast slopes, and the pinyon zone is wide, extending to 2650 m at the top of the highest peak. The breeding avifauna has responded to these differences. The complement of species that normally lives in pinyon of usual form and spacing is present, and several kinds of birds that typically avoid this plant formation breed in the most luxuriant stands. Evidently the latter species are attracted to physiognomic features of the pinyons that resemble those of the coniferous forest they ordinarily inhabit. Furthermore, at least three additional species that otherwise would be absent occur in the cool upper reaches of the zone, apparently responding there to preferred or required summer temperature regimes. I also have noted similar occurrences of birds in unusually dominant pinyon woodland in the Kawich Mountains of central Nye County, 100 km north-northeast of the Grapevines (Johnson 1956).

In recent years I have explored additional areas of heavy pinyon that invite avifaunal comparison with the groves in the Grapevines. These stands of old trees grow locally, in Nevada near the California line, in the Palmetto Mountains (= Mount Magruder plus the Silver Peak Mountains), Esmeralda County; the Wassuk Range, Mineral County; the Pine Grove Hills, Lyon County; and in the Sweetwater Mountains, Douglas and Lyon counties. In each of these regions, open woodlands of small trees and stands of intermediate height and density predominate on most slopes; the forests are more local in distribution.

For purposes of comparison of the avifaunas, it is useful to consider these several pinyon areas as comprising (1) a northern subset occupying the spur ranges connected to the east side of the Sierra Nevada, which includes the Wassuk and Sweetwater mountains and the Pine Grove Hills, and (2) a southern subset of wooded islands lying to the southeast, including the Palmetto and Grapevine mountains. The massive White Mountains lie between the two groups. The northern and southern subsets (Fig. 1) permit comparison of avifaunas along a northwest to southeast gradient. Some striking differences in avifaunal composition and numerical relationships of species emerge (Table 2). Although the northern and southern localities are only 90 km apart, several species reach their distributional limits between these mountain systems and thus breed in only one of the two regions. Unexpectedly, 19 species change in average population density along the gradient. For some (e.g., *Empidonax wrightii*), the change is subtle. For others (e.g., *Vireo solitarius*) population densities are dramatically different between northern and southern mountains.

Several species partly or completely switch habitats. For example, *Thryomanes bewickii* and *Otus asio*, common and uncommon residents, respectively, in the pinyon woodlands of the southern Great Basin and northern Mojave Desert, prefer riparian

cottonwoods and willow in west-central Nevada. Although both species use pinyon at the more northerly sites, the wren is uncommon, and the owl is rare in this association. *Empidonax wrightii* nests in tall sagebrush, bitterbrush, and juniper in the northwestern Great Basin where pinyon is lacking but is scarce or absent in such vegetation in southern Nevada. In other species the habitat change is more subtle. *Parus inornatus* and *Dendroica nigrescens* inhabit pinyon in both northern and southern localities, but their numbers diminish in the north where they prefer the more arid and warmer portions of the pinyon belt. In 5 of the 19 species, the change in density between north and south coincides with a shift in subspecific status and, in 3 species, with a concurrent change in habitat preference (Table 2).

How are we to interpret these contrasts in the avifaunas of the pinyon association of closely adjacent geographic regions? Two interrelated issues, (1) variation in the climatic aspects of the pinyon zone environment and (2) temperature-moisture preference and distributional histories of the bird

TABLE 2. Species composition and numerical relationships of pinyon woodland avifaunas of spur ranges of the northern Sierra Nevada<sup>1</sup> versus those of montane islands to the southeast<sup>2</sup>. Boreal (B) and Austral (A) species are distinguished.

<b>Species present only in north:</b>	
<i>Glauclidium gnoma</i> <sup>3</sup> (B)	<i>Certhia familiaris</i> <sup>3</sup> (B)
<i>Sphyrapicus ruber</i> <sup>3</sup> (B)	<i>Myadestes townsendi</i> (B)
<i>Cyanocitta stelleri</i> (B)	
<b>Species present in both areas but more numerous in north:</b>	
<i>Aegolius acadicus</i> (B)	<i>Sialia currucoides</i> (B)
<i>Dendrocopos villosus</i> <sup>4</sup> (B)	<i>Piranga ludoviciana</i> (B)
<i>Tachycineta thalassina</i> (B)	<i>Carpodacus cassinii</i> (B)
<i>Parus gambel</i> <sup>4,5</sup> (B)	<i>Chlorura chlorura</i> (B)
<i>Sitta carolinensis</i> (B)	<i>Junco hyemalis</i> (B)
<b>Species present in both areas but more numerous in south:</b>	
<i>Otus asio</i> <sup>4,5</sup> (A)	<i>Thryomanes bewickii</i> <sup>4,5</sup> (A)
<i>Empidonax wrightii</i> <sup>5</sup> (A)	<i>Poliaptila caerulea</i> <sup>5</sup> (A)
<i>Aphelocoma coerulescens</i> (A)	<i>Vireo solitarius</i> (B)
<i>Psaltiriparus minimus</i> <sup>4</sup> (A)	
<b>Species present only in south:</b>	
<i>Regulus calendula</i> <sup>3</sup> (B)	<i>Icterus parisorum</i> (A)
<i>Vireo vicinior</i> (A)	<i>Junco caniceps</i> (B)

<sup>1</sup>Wassuk Range, Sweetwater Mountains, and Pine Grove Hills.

<sup>2</sup>Grapevine Mountains and Palmetto Mountains (= Mt. Magruder + Silver Peak Mountains).

<sup>3</sup>Breeds only very locally in pinyon woodland in the northern or southern mountains.

<sup>4</sup>Subspecies in north different from that in south.

<sup>5</sup>Partial or complete habitat shift from north to south.

species at northern and southern stations, may offer partial explanation.

From rainfall data for the nearby White Mountains and several other pinyon sites in the southwest, St. Andre et al. (1965) concluded that overall aridity characterizes this plant formation. Unfortunately, no moisture data exist for the pinyon zones in the ranges of special interest here. Nonetheless, pinyon certainly occupies a range of rainfall regimes, and the more northern sites, although still relatively arid, presumably have greater average rainfall than the southern sites. Temperature data also are scarce, except for the White Mountains. However, I can conclude at least that the upper part of the zone averages considerably cooler than the lower part, a fact readily apparent to the researcher working at different elevations in this region. The unusual upper extension of the pinyon zone in the White Mountains (St. Andre et al. 1965) and in the Grapevine Mountains (Miller 1946) would enhance temperature differences that normally exist between the different elevations. Finally, because of the difference in latitude, it is probable that the northern sites average cooler than the southern ones.

The climatic preferences and distributional backgrounds of the bird species agree closely with the groupings of Table 2. The 5 species confined to the north and all 10 forms that are more numerous in the north are Boreal species with distributional backgrounds associated with northern coniferous forests. In contrast, except for *Regulus calendula*, *Vireo solitarius*, and *Junco caniceps*, forms of Boreal derivation (Miller 1951), all the species present only in the south or reaching their greatest numbers in the southern pinyon areas are of Austral origin, having been associated in their distributional histories with southwestern pinyon or oak woodlands. I conclude that this major trend in composition and density of pinyon zone avifaunas along the Nevada-California border apparently results from the exchange along a temperature-moisture gradient of southern pinyon woodland species, adapted

principally to the warm and relatively arid portions of the zone, and northern species, adapted chiefly to the relatively cool and moist portions of the zone.

The origin of the bird species of the Wassuks, Sweetwaters, and Pine Grove Hills is of particular interest because the pinyon woods in these ranges directly contact the coniferous forests of the Sierra Nevada. For this reason, bird populations of the pine-fir zone of the east side of the latter range have had easy access to pinyon forests lying to the east. Ready access may be one reason why *Cyanocitta stelleri* and, locally, *Certhia familiaris* and *Sphyrapicus ruber* breed in pinyon in these areas. Otherwise these species are not known to nest in this formation. It is noteworthy that none of these forms inhabits the old pinyon groves in the Desatoya Mountains of central Nevada, presumably because of the great distance of this range from source populations.

Note that from the pool of 27 pinyon zone species, nearly identical total numbers of breeding forms, 23 and 24, respectively, are recorded for northern and southern stations. Such equivalence is significant. Importantly, no neat system of replacement or of switches in abundance by species with similar ecologic roles occurs along the gradient (Table 2). Instead, the evolution of community structure at various localities in the pinyon formation probably has involved more subtle adjustments among the species in foraging zones, food quality, and/or habitat preference. Those species of birds represented by different geographic races at northern and southern localities would be especially worthy of close study in this regard.

#### Gradients in Boreal Avifaunas

I recently discussed controls of richness of Boreal species on 11 sample areas in the Sierra Nevada, Cascades, and Rocky Mountains and on 20 mountaintop islands in the Intermountain Region (Johnson 1975). Here I wish to expand on portions of that analysis through examination of both longitudinal and latitudinal trends in numbers of species



occupying particular Boreal habitats along four transects across the Great Basin. These transects (Fig. 3, lines I-IV) are roughly equidistant latitudinally and pass through 20 of the sample areas described in my previous paper. Species numbers now have been determined for eight additional areas, and these new data are included. Transect III fails to cross the entire Intermountain Region because no species lists are available for restricted portions of the main Rocky Mountains directly east of the Snake Range in eastern Nevada.

*Total species richness.*— All transects demonstrate the abrupt drop in total numbers of species in the north-south-oriented swath that extends across much of western and central Nevada (Fig. 4A). From high species totals of 56 to 64 at Mt. Shasta,

Lassen, Tahoe, and Yosemite, species richness declines sharply along transect I, between Warner and Pine Forest; along transect II, between Lassen and West Humboldt; along transect III, between Carson and Pine Nut; and along transect IV, between Yosemite and Glass Mountain. Species numbers then climb toward the east to totals of 56 and 55 at Uinta and Aquarius-Boulder, respectively, at the ends of the transects. Highest totals for the Sierra Nevada-Cascades always equal or exceed those for the Rocky Mountains. In the region of general impoverishment along each transect, a mountain range moderately rich in Boreal species interrupts the general smoothness of each species density curve (Fig. 4A): I, Jarbidge; II, Ruby; III, Toiyabe-Shoshone; and IV, White-Inyo.

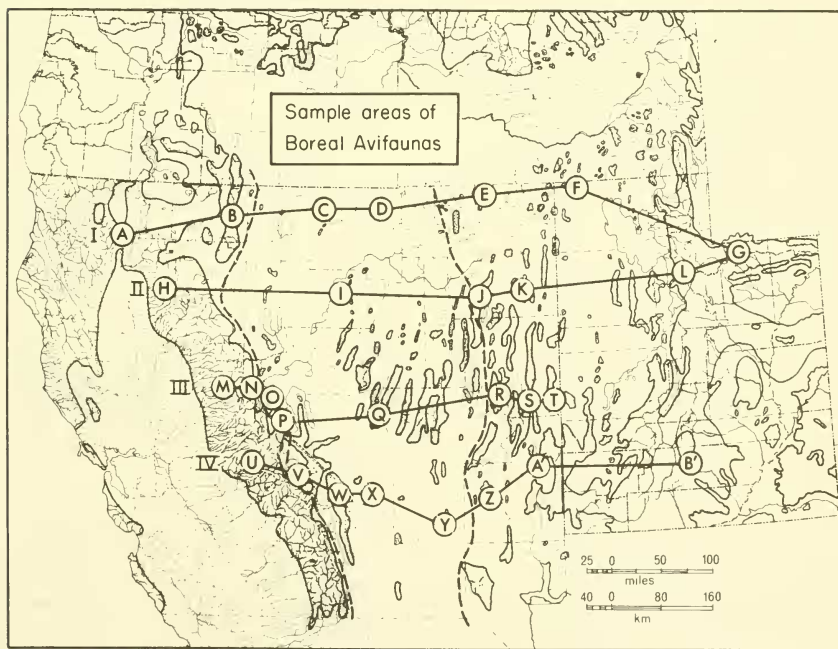


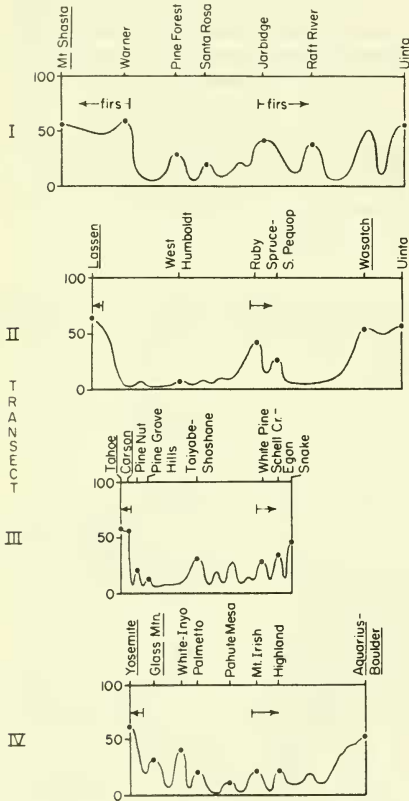
Fig. 3. Four transects across the Intermountain Region, passing through 28 sample areas of Boreal avifaunas. These sample areas are named in Fig. 4. No native firs are known to occur between the two vertical dashed lines.



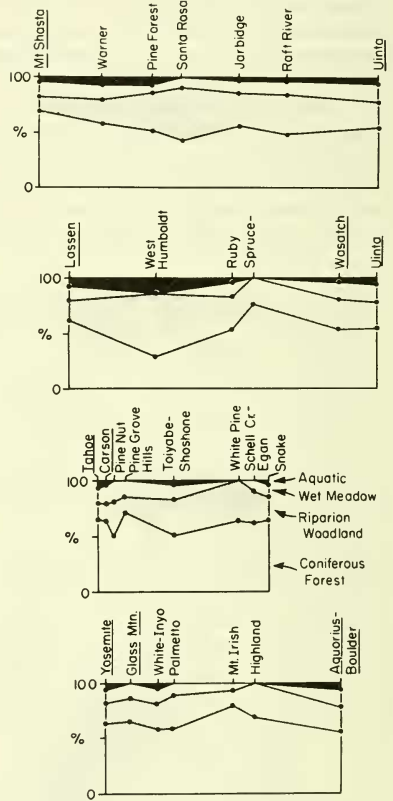
*Species richness according to habitat.*— In Figure 4B I portray the percentage of Boreal species in each of four major habitats (Johnson 1975: 549), i.e., Aquatic, Wet Meadow, Riparian Woodland, and Coniferous Forest. This permits study of possible changes along gradients of proportions of species preferring these habitats. For

each transect I have calculated the average percentage of species in each of the four habitats for Sierra Nevada-Cascades samples, Great Basin Islands samples, and Rocky Mountains samples (Table 3).

Between-transect comparisons of proportions of species in continental samples indicate striking similarities. For example,



A. Boreal bird species richness



B. Composition of boreal avifaunas

Fig. 4. Numbers of Boreal bird species (left) and percent avifaunal composition by four major habitats (right) along four transects across the Intermountain Region. Continental sample areas are underlined; island sample areas are not. Twenty sample areas are described more fully in Johnson (1975). Species totals for eight new ones added are as follows: A, Mt. Shasta (Grinnell and Miller 1944); I, West Humboldt Range (author's unpubl. data); L, Wasatch (Behle and Perry 1975); M, Tahoe (Orr and Moffitt 1971); O, Pine Nut Mtns. (author's unpubl. data); R, White Pine Mtns. (author's unpubl. data); S, Schell Creek-Egan Ranges (author's unpubl. data); and Y, Pahute Mesa (Hayward et al. 1963).

number of species in coniferous forests varies only from 62.5 to 69.6 percent of the total Boreal avifauna in the Sierra Nevada-Cascades, and those of riparian woodland vary only from 23.2 to 24.6 percent in the several samples from the Rocky Mountains. Other habitats on continents illustrate similar uniformity. Island samples are more complex and show differences among transects. Specifically, the island samples of transects I and II have proportionately more aquatic and riparian woodland species, but fewer coniferous forest species, than those of transects III and IV.

Within-transect comparisons (transects I, II, and III) point to more riparian woodland species and fewer coniferous forest species in samples for the Great Basin Islands versus the Sierra Nevada or the Rocky Mountains. However, the ecologic preferences of

birds in island samples resemble those of birds in Rocky Mountains samples more than those of forms in the Sierra Nevada-Cascades. The avifaunas of transect IV do not follow the pattern of the first three in that the proportions of species in the several major habitats are similar among samples of the Sierra Nevada, Great Basin, and Rocky Mountains.

*The composition of coniferous forest avifaunas.*— The fraction of coniferous forest bird species deserves special comment because some of the trends in total species richness discussed earlier are explained partly by the distribution of suitable tree species. The following group of forest bird species, distributed discontinuously in the Intermountain Region, illustrates this point: *Sphyrapicus varius*, *Sphyrapicus thyroideus*, *Empidonax hammondi*, *Empidonax difficilis*,

TABLE 3. Average percent composition, according to habitat preferences, of species in avifaunas along transects.

	SIERRA NEVADA-CASCADES CONTINENT (Mt. Shasta)	GREAT BASIN ISLANDS (Warner through Raft River)	ROCKY MOUNTAINS CONTINENT (Uinta)
Transect I			
Aquatic	3.6	3.7	5.3
Wet Meadow	12.5	10.8	16.1
Riparian Woodland	14.3	34.0	23.2
Coniferous Forest	69.6	51.5	55.4
Transect II	(Lassen)	(W Humboldt through Spruce-S. Pequop)	(Wasatch and Uinta)
Aquatic	7.8	6.3	3.6
Wet Meadow	12.5	4.0	17.3
Riparian Woodland	17.2	37.1	24.6
Coniferous Forest	62.5	52.6	54.6
Transect III	(Tahoe and Carson)	(Pine Nut through Snake)	
Aquatic	4.4	0.9	—
Wet Meadow	14.8	10.8	—
Riparian Woodland	16.5	27.4	—
Coniferous Forest	64.4	60.9	—
Transect IV	(Yosemite and Glass Mountain)	(White-Inyo through Highland)	(Aquarius- Boulder)
Aquatic	2.3	0.6	3.7
Wet Meadow	12.3	7.0	14.5
Riparian Woodland	19.0	23.4	23.6
Coniferous Forest	66.4	69.0	58.2

*Sitta canadensis*, *Certhia familiaris*, *Regulus satrapa*, *Regulus calendula*, *Hesperiphona vespertina*, and *Spinus pinus*. Although most of these forms occasionally breed in other kinds of conifers or in deciduous trees, they prefer firs (*Abies concolor* or *Pseudotsuga menziesii*) and avoid or nest sparingly in forests lacking these trees. Thus, the distribution of firs in the Intermountain Region is of special significance for these species. Figure 4A indicates the presence of firs in the various sample areas. Note the repeated instances of increased numbers of species, of all kinds of birds and of coniferous forest birds, in relation to the appearance of firs.

Firs are absent from the zone of avifaunal impoverishment across western and central Nevada (Fig. 3). Although skimpy clumps grow in the Sweetwater Mountains, no firs occur in any of the other ranges along the California-Nevada border southeast of the Carson Range. Firs reappear in eastern Nevada between 115° and 116° W Longitude. Among the ranges considered here, substantial stands occur in the Jarbidge Mountains, White Pine Mountains, and on Mount Irish. Critchfield and Allenbaugh (1969) report white fir locally in the Ruby Mountains, but the avifauna at that site has not been explored.

Bristlecone pine (*Pinus longaeva*) dominates the upper slopes of several ranges in eastern Nevada. This tree is important for coniferous forest birds in part because it occasionally forms closed, well-shaded stands with strong physiognomic resemblance to firs. Apparently in response to this feature, several kinds of birds from the above list often occupy well-developed bristlecone pine forests when firs are scarce or lacking. The two species of *Sphyrapicus*, *Empidonax difficilis*, *Sitta canadensis*, and *Regulus calendula* exemplify this point. In Nevada, the best stands of this conifer grow east of the right vertical dashed line on Figure 3 that marks the boundary of white fir distribution, and in many places the two species occur in mixed stands.

#### BREEDING RANGE BOUNDARIES AND INTERSPECIFIC DISTRIBUTIONAL RELATIONSHIPS

Broad trends in avian geography are best identified through comparison of major components of avifaunas. Other, more detailed issues can be seen most clearly by inspection of the distributions of single species and their close relatives. Here I discuss four contrasting examples, chosen from a long list of possible cases, that illustrate particular species-level distributional phenomena occurring among birds of the Intermountain Region. Three of these examples also support the view offered earlier that this region presently serves as an important arena of disjunction, contact, and intermixture of species representing avifaunas of differing geographic derivation.

*Grace's Warbler and ponderosa pine.*—In southeastern Nevada, as in the southern Rocky Mountains generally, Grace's Warbler (*Dendroica graciae*) breeds commonly and exclusively in forests of ponderosa pine (*Pinus ponderosa*). But near the northwestern edge of the occurrence of the Rocky Mountain form of the ponderosa pine (*P. ponderosa* var. *scopulorum*), for example in the Quinn Canyon Range, the scattered and stunted trees occupy marginal sites, and the bird is rare. It is absent from the few ponderosas that grow locally in the Highland Range, on Mount Wilson, and in the southern White Pine Mountains, and, farther north, from the extensive ponderosa pine habitat in the Snake Range (Fig. 5).

This case is particularly interesting because prior to 1963 the Grace's Warbler was not known to breed anywhere in southern Nevada. Since then, numerous records have been obtained, several from places that previously had been well-explored (Johnson 1965, 1973, 1974). Therefore, the evidence points to an active northwestward range expansion in the past decade or two. Although further extension into presently unoccupied ponderosa pine habitat is possible, total distributional evidence suggests

that the approximate northwestern limit in the Intermountain Region already has been reached. However, given continued range expansion, eventual colonization of the arid ponderosa pine forests of southern California seems probable, for the species is already vagrant to that area, and a number of other species of the interior Southwest have become established there in recent years (Johnson and Garrett 1974). Insofar as is known, Grace's Warbler has never nested in the vast ponderosa pine forests of the central and northern Rockies, or in the Sierra Nevada.

The warbler thus illustrates two biogeographic phenomena typically seen in species with well-documented distributions: (1) the actual range falls short of the geographic extent of seemingly appropriate habitat and (2) the distributional boundaries are unstable because of their complex con-

trol by a multiplicity of interacting factors that are themselves fluctuating. I wish to emphasize that no other species of warbler or other pine-foliage insectivore obviously competes with *D. graciae* and, for this reason, has adjusted its distribution and abundance as a result of recent population interaction with that species. Instead, the northwestern distributional perimeter of Grace's Warbler seems to be set by other aspects of the environment. For example, this warbler may be dependent upon populations of pine arthropods that fluctuate in annual density, especially near the periphery of their ranges. Or, summer temperature and moisture barriers dictated by the metabolic requirements and preferences of the warbler, the arthropods upon which it feeds, or the pines they both inhabit, may control the range border. I have no data to support a convincing explanation.

*Downy Woodpecker and Ladder-backed Woodpecker in disjunct allopatry.*— These two congeners fail to contact in the Great Basin. The Downy inhabits aspen groves in the northern and eastern mountains (the form *D. p. leucurus*), or cottonwoods and willows along rivers in west-central Nevada (the form *D. p. turati*), and the Ladder-back lives in the cottonwood-willow association in valleys or Joshua tree woodland in the Mojave Desert. Unexpectedly, substantial areas of apparently suitable habitat occur in the wide zone now unoccupied by either species. Thus, the Downy Woodpecker has not been found in the fine aspen woodland in the Schell Creek Range or on Mount Wilson, among a number of seemingly appropriate places. Similarly, the Ladder-back avoids considerable Joshua tree growth in Esmeralda and Nye Counties, Nevada. Finally, neither species breeds in the excellent riparian woods in Owens Valley, although the Ladder-back has been recorded at Lone Pine, at the foot of the valley (Grinnell and Miller 1944). I conclude that the respective southern and northern limits of these two species, within suitable habitats, are dictated primarily by temperature and mois-

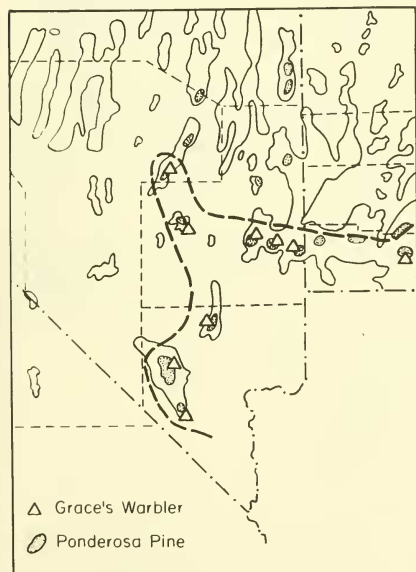


Fig. 5. Approximate breeding distribution of Grace's Warbler (triangles) and occurrence of ponderosa pine (stippled areas) in southeastern Nevada and southwestern Utah. Lower elevational perimeters of woodlands in mountains also are indicated.

ture. Considering the wide unoccupied swath between their ranges in the central Intermountain Region, distributional limits there certainly are not controlled by interspecific competition.

*Mountain Bluebird and Western Bluebird in parapatry.*— These two congeneric thrushes (*Sialia currucoides* and *S. mexicana*, respectively) breed in contiguous allopatry, or parapatry, in much of the southern Intermountain Region. One might conclude that such a distributional relationship is the result of interspecific competition (Fig. 6). In at least three general areas where both species have been recorded (Panamint Range, Delamar Range, Zion National Park), their spatial relationships are unclear. But, because of their well-known differences in habitat preference (Grinnell and Miller 1944), competitive interaction probably is infrequent or absent, given a situation of local sympatry. Until more details are available, I conclude that the striking parapatry results from the geographic position of a

sharp shift in average spring and summer temperatures. The approximate coincidence of the zone of parapatry with the northern limits of the Mojave Desert supports this suggestion.

*Hammond's Flycatcher and Western Flycatcher in broad sympatry.*— As in the previous examples, this case also concerns a species of northern derivation, Hammond's Flycatcher (*Empidonax hammondi*), and a congener of southern derivation, the Western Flycatcher (*E. difficilis*). These two forms offer a particularly impressive example of how the complex interplay of phylogenetic and distributional history has influenced present-day habitat selection and ecologic interaction. Figure 7 shows the distributional and numerical relationships of these species in western North America.

Hammond's Flycatcher is commonest in cool, moist Boreal forests of the Sierra Nevada, Cascades, and Rocky Mountains; its principal range therefore surrounds the Intermountain Region on three sides. In con-

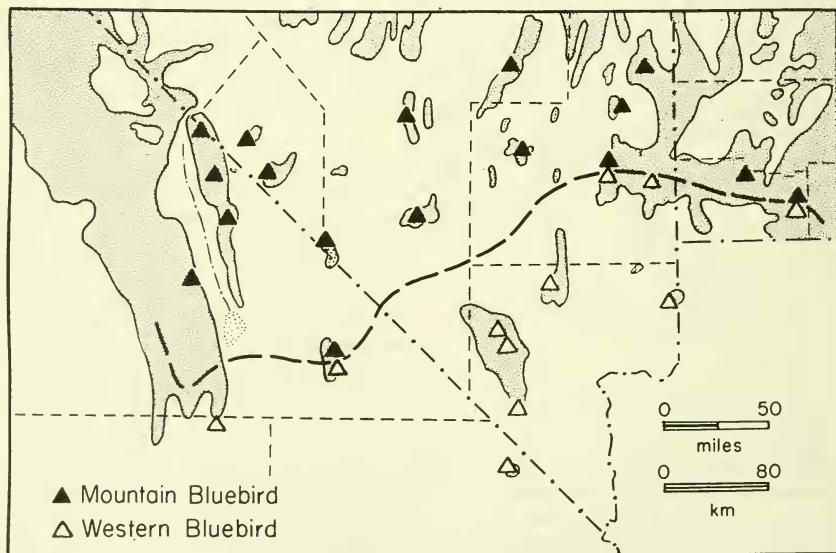


Fig. 6. Breeding distributional relationship of the Mountain Bluebird (*Sialia currucoides*) and Western Bluebird (*S. mexicana bairdi*) in southern Nevada and adjacent states.



trast, the Western Flycatcher reaches its greatest densities in warm Pacific Coastal forests (small form *E. d. difficilis*) and in arid interior highland forests of the Intermountain Region and southern Rocky

Mountains of Arizona and New Mexico (large form *E. d. hellmayri*), where *E. hammondii* is either absent or rare and local. In areas of contact between Hammond's Flycatcher and the similarly sized *E. d. diffi-*

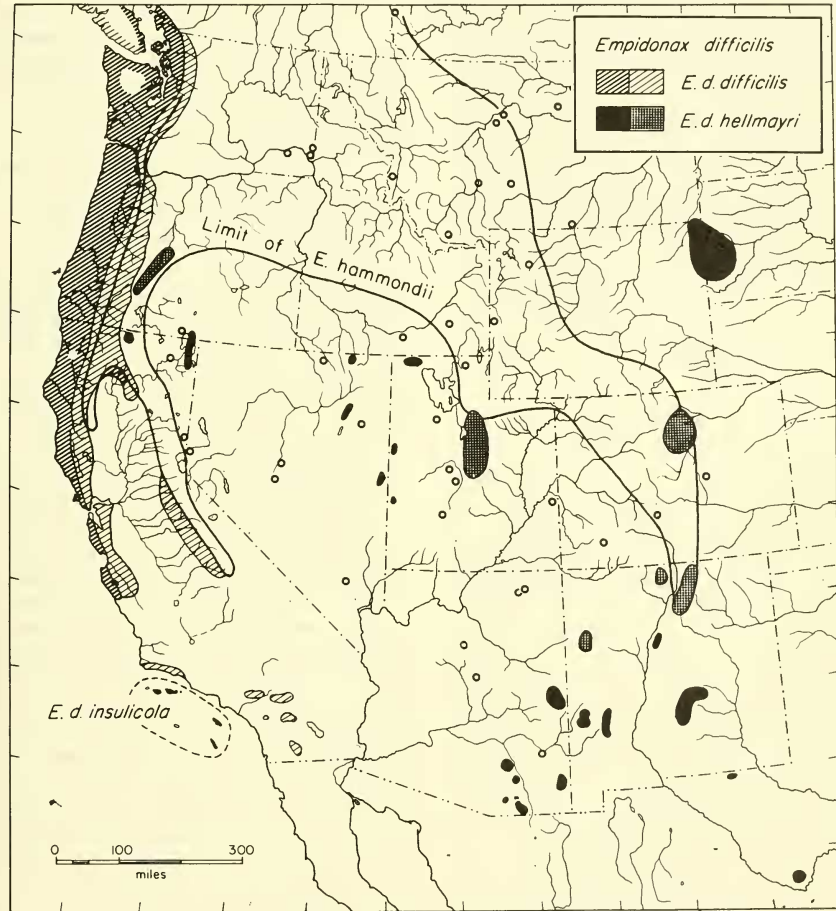


Fig. 7. Breeding distributional relationship of Hammond's Flycatcher (principal range outlined) and Western Flycatcher in the contiguous western United States. Relative abundance of three forms of Western Flycatcher is shown by patterns as follows: *E. d. difficilis*, heavy slanted lines indicate very common to abundant populations, and light slanted lines indicate common to uncommon populations; *E. d. hellmayri*, black indicates very common to abundant populations, and dotted pattern indicates common to uncommon populations. *E. d. insulicola* is common to abundant on the California Channel Islands, indicated in black. Scattered localities for *F. d. hellmayri* are shown by circles; note that many of them occur within the main range of *E. hammondii*. A few localities for the latter species, located south of the main range, are omitted.

*cilis* in the Pacific Northwest and on the west side of the Cascades, interspecific territories are defended (Johnson 1966 and unpubl. data). In the Rockies of southern Colorado the larger *E. d. hellmayri* evidently overlaps in territories with *E. hammondi* (Beaver and Baldwin 1975). The important point is that these two species are largely allopatric; considering the bulk of their numbers, this results directly from selection of similar, though not identical, habitats in different major climatic zones. Where they overlap, one species is nearly always common, the other uncommon or rare. Despite the geographic shifts in relative abundance and subtle differences in habitat selection, which presumably are consequences of millennia of competitive interaction, the two species do occur sympatrically in many places. Obviously one species has not limited the geographic range of the other (Fig. 7).

Within the genus *Empidonax*, these two species are separated phylogenetically by a series of other forms of closer relationship. The Hammond's Flycatcher is allied to the Least Flycatcher (*E. minimus*) and to other species of Boreal derivation (Johnson 1963). The Western Flycatcher, in contrast, is closest to Neotropical montane stocks such as *E. flavescens* and is certainly of southern derivation (N. K. Johnson, unpubl.). Apparently such evolutionary backgrounds have permitted extensive convergence in habitat preference and foraging ecology, for in the western United States, *E. hammondi* and *E. difficilis* are the commonest *Empidonax*es of dense coniferous forest.

#### Controls of Boundaries of Species' Ranges

The previous accounts offer only the barest introduction to the vast subject of the determinants of borders of breeding distributions of birds. Nonetheless, it is appropriate to comment briefly on this topic because it lies at the heart of biogeography and because of significant trends in the pertinent literature.

Grinnell (1914, 1917) and Bartholomew (1958), among others, have emphasized manifold controls of distributional boundaries of animal species, with the importance of particular factors changing along the range perimeter. They favored niche requirements and physiologic-climatic preferences as the crucial dictates of species distributions; interspecific competition either was not mentioned or its relevance was subordinated. In the more recent literature of ornithological ecology, the limitation of geographic range through competitive exclusion has become a prominent theme (MacArthur 1972, Cody 1974). However, the invocation of competition in this context has been premature.

In agreement with Salt (1952), whose classic paper clearly describes how metabolism and climate interrelate to control the distributions of three species of finches (*Carpodacus*), I see little reason to postulate competition as an effective determinant of range borders of species of birds in the Intermountain Region. The question is not whether competition occurs among the many overlapping species here; rather, it is what form does this competition take, and, as such, can it influence range boundaries? From all the evidence I have seen, including that from the four examples discussed, competition probably has had little influence in the determination of range boundaries of birds. Instead, alterations in density, such as shown for the two species of *Empidonax*, are the more likely outcomes of competitive interactions. Finally, I suggest that it is unwise to conclude that boundaries of tropical species are set by competition (Terborgh and Weske 1975), in the virtual absence of data on the occurrence of those environmental requisites crucially related to the distribution of the bird species in question.

#### PATTERNS OF AVIAN SPECIATION IN THE INTERMOUNTAIN REGION

In this section I concentrate on what I consider to be active zones of speciation in

the Great Basin region. These are illustrated by currently interacting populations of closely related taxa, well-differentiated at various levels above that of the incipient subspecies. For those concerned with more subtle examples of racial differentiation in this region, Behle (1963) provides a useful review. Information on speciation zones is of significance to the data previously presented on avifaunal gradients because of the great probability that the same environmental discontinuities in climate and flora ultimately are responsible for both.

### Zones of Intergradation, Disjunction, and Secondary Sympatry

Birds demonstrate a particularly wide range of speciation phenomena along the western edge of the Great Basin, in a zone extending south-southeastward from southern Oregon to southeastern California and southern Nevada. Indeed, there is evidence from the general distribution and speciation of birds in western North America that the zone just delineated is actually part of a larger biotic separation that extends northward to British Columbia and beyond. Here I wish to discuss 16 selected pairs of taxa (Table 4) in the western Intermountain Region that illustrate stages in the speciation process. Figure 8 schematically portrays zones of intergradation and hybridization for nine of these pairs of taxa.

Several patterns emerge from study of this wealth of material. The first concerns the striking, although imprecise, geographic coincidence of the several contact zones that link (or divide) coastal and interior populations. Secondly, a large number of species are represented, suggesting that significant environmental gradients or discontinuities in the western Great Basin pervasively influenced the differentiation of birds. Indeed, few other regions in North America can claim a comparable diversity of speciation phenomena within such restricted geographic limits.

Furthermore, the interacting taxa of nearly every pair occupy different habitats

on each side of the contact zone (Table 5). Habitats in the contact areas themselves are typically intermediate between coastal and interior situations. In a major trend illustrated by six pairs of taxa, the coastal representative inhabits coniferous forest or oak

TABLE 4. Examples of coastal or Sierra Nevada and interior taxa that illustrate speciation phenomena along the interface of the Cascades-Sierra Nevada and Great Basin.

#### Gradual primary integradation; racial boundaries weak<sup>1</sup>:

1. *Sphyrapicus thyroideus thyroideus* and *S. t. nataliae*. Williamson's Sapsucker.

#### Narrow zone(s) of primary or secondary intergradation between representatives of strongly divergent racial complexes:

2. *Empidonax difficilis difficilis* and *E. d. helmayri*<sup>2</sup>. Western Flycatcher.
3. *Eremophila alpestris sierrae* and *E. a. lamprochroma*. Horned Lark.
4. *Aphelocoma coerulescens superciliosa* and *A. c. nevadae*. Scrub Jay.
5. *Saltriparus minimus californicus* and *P. m. plumbeus* or *P. m. providentialis*. Bush-tit.
6. *Amphispiza belli canescens* and *A. b. nevadensis*. Sage Sparrow.
7. *Passerella iliaca megarhynchus* and *P. i. fulva* or *P. i. monoensis*. Fox Sparrow.
8. *Dendrocopos pubescens turati* and *D. p. leucurus*. Downy Woodpecker.

#### Disjunct allopatry between representatives of strongly divergent racial complexes:

9. *Parus inornatus inornatus* or *P. i. kernensis* and *P. i. zaleptus*. Plain Titmouse.
10. *Vireo solitarius cassinii* and *V. s. plumbeus*. Solitary Vireo.
11. *Vermicora celata lutescens* and *V. c. orestera*. Orange-crowned Warbler.

#### Narrow zone or sympatry and interspecific hybridization:

12. *Sphyrapicus ruber daggetti*. Red-breasted Sapsucker and *S. varius nuchalis*. Red-naped Sapsucker.
13. *Junco hyemalis thurberi*. Dark-eyed (Oregon) Junco and *J. caniceps caniceps*. Gray-headed Junco.

#### Disjunct allopatry between species:

14. *Pica nuttalli*. Yellow-billed Magpie and *P. pica hudsonia*. Black-billed Magpie.
15. *Vermicora ruficapilla ridgwayi*. Nashville Warbler and *V. virginiae*. Virginia's Warbler.
16. *Leucosticte tephrocotis dawsoni*. Gray-crowned Rosy Finch and *L. atrata*. Black Rosy Finch.

<sup>1</sup>Many additional examples of this category could be cited (see Behle 1963).

<sup>2</sup>In each pair of taxa the coastal-Sierran form precedes the interior form.

TABLE 5. Habitat preferences and contact zones of taxa listed in Table 4.

SPECIES <sup>1</sup>	HABITAT OF COASTAL <sup>2</sup> OR SIERRAN FORM	HABITAT OF INTERIOR FORM	ZONE(S) OF CONTACT OR APPROACH OF TAXA	SOURCE
1. Williamson's Sapsucker	Mixed coniferous forest.	Mixed pine-fir, especially white fir- bristlecone pine.	Warner Mtns. area.	N. K. Johnson (1970).
2. Western Flycatcher	Canyon-bottom woodlands or forests in lowlands and foothills.	Riparian woodlands or forests in high- lands.	Siskiyou Mtns. area.	N. K. Johnson, unpubl.
3. Horned Lark	Large mountain meadows surrounded by conifers.	Playas surrounded by sparse desert scrub.	Sierra Valley, Plumas Co., Calif.	Behle (1942).
4. Scrub Jay	Oak woodland and chaparral.	Pinyon-juniper woodland.	Douglas Co., Nev.; E slope southern Sierra Nevada in Inyo Co., Calif.	Pitelka (1951).
5. Bush-tit	Evergreen oak-chaparral.	Pinyon-juniper and mountain mahogany woodland.	Lassen Co., and E slope southern Sierra Nevada, Inyo Co., Calif.	Grinnell, Dixon, and Linsdale (1930); Swarth (1914).
6. Sage Sparrow	Mixed brushland of <i>Artemisia</i> with much <i>Atriplex</i> .	Sagebrush scrub; some <i>Atriplex</i> .	Mono Co., Calif.	Grinnell and Miller (1944).
7. Fox Sparrow	Brushland of <i>Ceanothus</i> and <i>Arctostaphylos</i> . Less commonly, riparian thickets.	Riparian thickets of willows, aspens, birches, and alder; less commonly, brushland.	Modoc-Lassen Cos., and Alpine-Mono- Inyo Cos., Calif.	Grinnell and Miller (1944).
8. Downy Woodpecker	Willows and cottonwoods in lowlands and foothills.	Aspen and cottonwoods in mountains.	Modoc Plateau.	Grinnell and Miller (1944).
9. Plain Titmouse	Oak woodland.	Pinyon-juniper woodland.	No known contact; ranges divided by Sierra Nevada.	Grinnell and Miller (1944).

10. Solitary Vireo	Dry and warm conifer and oak forests.	Pinyon-juniper woodland.	No known contact. Forms approach to within 50 km in vicinity Alpine Co., Calif. and Lyon Co., Nev.	N. K. Johnson, unpubl.
11. Orange-crowned Warbler	Mixed oak woodland-chaparral.	Aspen woodland.	Forms approach in vicinity of Alpine Co.-Mono Co. border.	Grinnell and Miller (1944).
12. Red-breasted and Red-naped Sapsuckers	Mixed coniferous forest and woodland.	Aspen woodland; also white firs.	Warner Mtns., Modoc Co., Calif.; Mono Co., Calif. and Lyon Co. and Mineral Co., Nevada.	Howell (1952); N. K. Johnson, unpubl.
13. Dark-eyed (Oregon) and Gray-headed Juncos	Open coniferous forest with grassy openings.	Dense pinyon and/or mountain mahogany woodland with grass or herbs on shaded floor.	Mountains along state line between Mono Co. and San Bernardino Co., Calif.	Miller (1941); N. K. Johnson, unpubl.
14. Yellow-billed and Black-billed Magpies	Pasture lands with clumps of trees.	Stream and lake valleys with clumps of willow or <i>Shepherdia</i> .	No contact; ranges separated by axis of Cascades and Sierra Nevada.	Grinnell and Miller (1944).
15. Nashville and Virginia's Warblers	Oak-conifer woodland with brushy understory.	Pinyon or scrub oak woodland.	No contact; ranges approach along Calif.-Nev. border SE of Lake Tahoe.	N. K. Johnson, 1976.
16. Gray-crowned and Black Rosy Finches	Alpine cirques and meadows.	Alpine cliffs and adjacent turf.	No contact in area of this study. Absent in summer in wide swath across W and Cent. Nev.	R. E. Johnson (1975).

<sup>1</sup>For ease of comparison, the species are listed according to the sequence of Table 4.

<sup>2</sup>The principal kind of habitat occupied in most places is described. Any form listed here may breed uncommonly or rarely in somewhat different habitats.



woodland-chaparral, and the interior race or species lives in pinyon-juniper woodland. In four additional pairs of taxa, the coastal or Sierran form occupies oak-chaparral, coniferous forest, or brush associated with such forest, and the interior form switches to riparian aspen or willows. Earlier I discussed the latter trend (Johnson 1970).

In 5 of the 16 pairs, the coastal and interior representatives are disjunct, with ranges separated by gaps that overlap or straddle many of the zones of intergradation of the 11 pairs of forms that do contact. Evidently the intervening habitat separating the disjunct forms is unsuitable for these particular species. Seven of the 11 pairs that meet and interact occur less commonly in the contact zone than in the adjacent regions. This

clearly suggests that population densities are reduced for several species in and near their zones of intergradation. Thus, the environments at the western border of the Intermountain Region are unsuitable for certain species and marginal for others. In any case, the variety of distributional and speciation phenomena represented underscores the steep environmental gradients that influence selection pressures on bird populations in the restricted zone where the Cascade Mountains and Sierra Nevada meet the Great Basin. Munz and Keck (1968), Baldwin (1973), and Miller (1951) describe the significant physiographic, floristic, and climatic changes ultimately responsible for the evolution of contrasting avifaunas in this region.

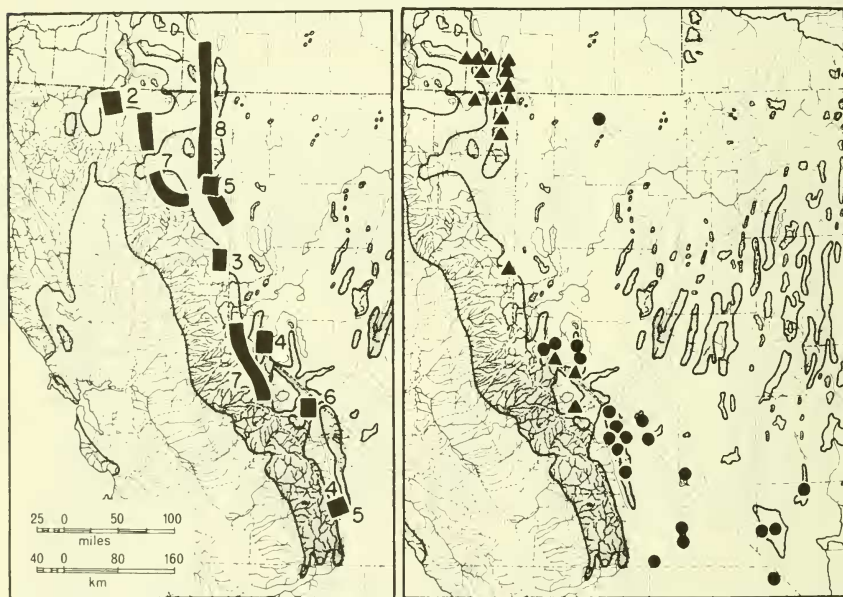


Fig. 8. Left, zones of primary intergradation and hybridization (secondary contact), at the western border of the Great Basin, in seven species of birds. Numbers correspond to those in Table 4: 2, Western Flycatcher; 3, Horned Lark; 4, Scrub Jay (two zones); 5, Bush-tit (two zones, one of which is identical with a zone of the Scrub Jay); 6, Sage Sparrow; 7, Fox Sparrow (two zones); and 8, Downy Woodpecker. Right, localities of sympatry and hybridization between Red-breasted and Red-naped Sapsuckers (triangles) and between Dark-eyed (Oregon) and Gray-headed Juncos (dots).

# Physiographic Breaks and Avifaunal Boundaries

A major gap in the mountain systems of the western United States results from the low trough that begins in southeastern Oregon, courses southward through western Nevada, veers southeastward between Walker Lake and the Paradise Range, then continues through the Death Valley area and beyond into the Mojave and Colorado deserts. With such a geographic position, it would be easy to assume that this trough separates the Boreal avifaunas of the Cascades and Sierra Nevada from those of the interior. However, this is not the case, for a host of interior races and species of birds occur westward to the Warner, Wassuk, Sweetwater, and White mountains. These interior forms therefore maintain popu-

lations on the west side of the trough at localities well-removed from their principal centers of distribution from central Nevada eastward. These occurrences provide clear evidence for the suitability, for at least some interior species, of those montane environments located directly adjacent to the southern Cascades and east side of the Sierra Nevada. But these same ranges also host many Cascadian and Sierran forms that have colonized from the west. Thus, peculiarly intermixed avifaunas breed in all four mountain systems (Table 6). One of the four ranges, the Sweetwaters, has only a minor representation of interior forms; the others have numerous Great Basin-Rocky Mountain species. All of the other mountain systems along the Nevada-California border, the Carson Range, Pine Nut Mountains, Pine Grove Hills, and Glass Mountain, lack inte-

TABLE 6. Intermixture of Cascade-Sierra Nevada and interior components<sup>1</sup> in Boreal avifaunas of mountain ranges<sup>2</sup> along the western edge of the Great Basin.

CASCADE MOUNTAIN-SIERRA NEVADAN FORMS	WARNER MOUNTAINS	WASSUK RANGE	SWEETWATER MOUNTAINS	WHITE MOUNTAINS
<i>Dendragapus obscurus sierrae</i>	X	—	X	X
<i>Sphyrapicus ruber daggetti</i>	X	X	X	—
<i>Cyanocitta stelleri frontalis</i>	X	X	X	X
<i>Vireo solitarius cassinii</i>	X	—	—	—
<i>Vermivora ruficapilla ridgwayi</i>	X	—	—	—
<i>Wilsonia pusilla chryseola</i>	—	—	X	—
<i>Leucosticte tephrocotis dawsoni</i>	—	—	X	X
<i>Junco hyemalis thurberi</i>	X	X	X	X
<i>Passerella iliaca monoensis</i> <sup>3</sup>	—	X	X	—
GREAT BASIN-ROCKY MOUNTAIN FORMS				
<i>Selasphorus platycercus</i>	—	X	—	X
<i>Sphyrapicus varius nuchalis</i>	X	X	X	X
<i>Dendrocopos pubescens leucurus</i>	X	—	—	—
<i>Empidonax difficilis hellmayri</i>	X	—	—	— <sup>4</sup>
<i>Vireo solitarius plumbeus</i>	—	X	X	X
<i>Vermivora celata orestera</i>	X	—	—	X
<i>Vermivora virginiae</i>	—	X	—	X
<i>Wilsonia pusilla pileolata</i>	X	—	—	X
<i>Junco caniceps caniceps</i>	—	—	—	X
<i>Passerella iliaca fulva</i>	X	—	—	—
<i>Passerella iliaca canescens</i>	—	—	—	X

<sup>1</sup>Emphasis is on forms of contrasting Sierra Nevada versus interior distribution. Many undifferentiated species of widespread distribution in the western United States are not considered here.

<sup>2</sup>Sources of data: Warner Mountains, Miller (1951) and Johnson (1970); Wassuk Range, original data of author and few records from Linsdale (1936); Sweetwater Mountains, specimens in MVZ and original data of author; White Mountains, Grinnell and Miller (1944) and Miller and Russell (1956).

<sup>3</sup>The avifaunal relationships of this form are uncertain.

<sup>4</sup>Miller and Russell (1956) report *E. d. difficilis* in late June, but the bird was not certainly nesting even though the specimen was in breeding condition.

rior forms; their Boreal avifaunas are entirely comprised of Sierra Nevadan and widespread species. Because the most distinctive interior species and racial complexes, such as *Selasphorus platycercus*, *Vermivora virginiae*, and the *woodhouseii* Group of *Aphelocoma coerulescens*, extend all the way from eastern California to Colorado, there is no Boreal avifauna typical only of the Great Basin section of the interior.

The aforementioned distributional evidence thus supports the principal conclusion derived from the location of contact zones, namely, that the most trenchant separation of coastal-Sierran versus interior stocks occurs in a zone of varying width that runs southward just east of the crest of the Cascades then southeastward along the interface of the Sierra Nevada and Great Basin. Presumably it is the beginning of the precipitation shadow and the consequent shift from a coastal to an interior continental climate that provide the profound environmental transition responsible for this zone. The low desert trough to the east does not represent a significant avifaunal barrier.

*Epilogue.*—Avian geography in the Inter-mountain Region continues to progress, albeit cautiously, from the descriptive to the analytic phase. With only crude patterns now discernible, much remains to be learned and interpreted. But, heeding E. O. Wilson's (1970) reminder that "...biogeography is far and away the most difficult of all the biological sciences," I am inclined to treat with great kindness even those tentative patterns that so far have surfaced from the chaos.

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